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Earliest Triassic ichthyosaur fossils push back oceanic reptile origins

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Reptiles first radiated into oceanic environments after the cataclysmic end-Permian mass extinction (EPME)[1], 251.9 million years (Ma) ago. The geologically oldest fossils evincing this adaptive transition have been recovered from upper-Lower Triassic (lower Spathian) strata, ~248.8 Ma[2], and postdate a landmark turnover of amphibian-dominated to reptile-dominated marine ecosystems spanning the late Smithian crisis (LSC)[3], ~249.6 Ma[4] —less than ~2.3 Ma after the EPME. Here, we report ichthyopterygian (the group including 'fish-shaped' ichthyosaurians[1]) remains from the Arctic island of Spitsbergen that predate the LSC in later-middle to early-late Smithian[5] deposits up to ~250 Ma. Unexpectedly, however, their large size and spongy internal bone structure indicate a fully pelagic ichthyopterygian[1,6]. Given this unambiguous occurrence ~2 Ma after the EPME, these pioneering seagoing tetrapods can now be feasibly recast as mass extinction survivors instead of ecological successors[2,3] within the earliest Mesozoic marine predator communities.

The ichthyopterygian fossils (Natural History Museum, University of Oslo [PMO] 245.975) were found in the Lusitaniadalen Member (LM) of the Vikinghøgda Formation[7]. This unit crops out along Flowerdalen ('Flower's valley') on the lowermost slopes of Marmierfjellet ('Mt Marmier') in western Spitsbergen (Figure S1). The LM exposures form steep banks that are capped by gently sloping consolidated scree and topsoil with no immediately overlying younger strata. Lithologically, they comprise dark grey laminated shaly mudstone with abundant green-grey calcitic concretions (commonly septarian with baryte)[7] preserving a distinctive marine vertebrate fossil assemblage of temnospondyl amphibians, coelacanths, actinopterygian fishes, and euselachian sharks[3]. Collectively, this faunal horizon is termed the 'Fish Niveau'[8] and correlates with the middle Smithian *Euflemingites romunderi* zone, as well as the condensed lower-upper Smithian *Wasatchites tardus* zone[5,7]. The LSC immediately preceded the Smithian/Spathian boundary[4], which coincides with a regressive hiatus in sections from Marmierfjellet and in Ledalen on Botneheia, a mountain further to the west[5]. The sequentially overlying Vendomdalen Member (VM) records transgressive deeper water low-oxic conditions[7] and contains extremely fossiliferous faunal horizons. (1) The '*Grippia* Niveau' Bonebed[5] with small and large-bodied ichthyopterygians, basal ichthyosauromorphs (the clade encompassing ichthyopterygians, antecedent ichthyosauriforms and their more distant relatives[9]), presumably aquatic archosaurian reptiles, actinopterygians, and euselachains[3,8,10] that demarcate the lower to middle Spathian *Bajarunia euomphala* and *Parasibirites grambergi* zones[5]. (2) The 'Lower Saurian Niveau' with numerous large and small-bodied ichthyopterygians[8], basal ichthyosauromorphs[8], coelacanths, ceratodont lungfish, actinopterygians and euselachains represents the upper Spathian *Keyserlingites subrobustus* zone[5]. Characteristically, the VM shales are interspersed with conspicuous yellow-weathering ferric dolomite beds and concretions, although dark grey (or black in fresh cross-section) calcitic concretions are concentrated near the top of the member and stratigraphically correspond to the 'Lower Saurian Niveau'[5].

We used X-ray fluorescence (XRF) spectroscopy to geochemically compare the green-grey baryte infested calcitic matrix surrounding PMO 245.975 with both *in-situ* LM concretions collected elsewhere along Flowerdalen, and lithologically analogous VM concretions excavated up-sequence on Marmierfjellet (Figure 1A); thereby eliminating the possibility of down-scree transport. These analyses (Supplemental information) patently grouped PMO 245.975 with LM concretions sampled from the 'Fish Niveau', which integrate higher siliciclastic content (Si, Fe, Mn, K, Zr) denoting sandy sediment input[5]. By contrast, those from the 'Lower Saurian Niveau' have purer carbonate composition (Ca) and proportionately elevated vanadium (V) indicating decreased oxygenation[5]. This supports the interpretation of increasingly offshore conditions[5,7], as well as our field observation that PMO 245.975 had eroded directly from a restricted outcrop of LM mudstone before being broken up and dispersed by frost weathering.

PMO 245.975 consists of 11 articulated vertebral centra (Figure S2), together with 15 indeterminate bone fragments, perhaps from neural arches, limb and/or limb girdle elements. The centra are diagnostically amphicoelous with perforated notochordal canals and unfused neurocentral sutures[1]. Their articular surfaces are dorsoventrally elongate and hexagonal in outline unlike the cylindrical 'spool-shaped' centra of basal ichthyosauriforms[1]. Microtomographic (μCT) scans confirmed that the lateral centrum surfaces lack rib-bearing apophyses and that hemal arch facets are present on the ventral margins (Figure 1B), which is similar to early ichthyopterygian distal caudal vertebrae[10].

At ~60 mm high, ~30 mm long and ~40 mm in maximum width, the centra of PMO 245.975 are substantially larger than those of typical basal ichthyosauriforms[9,10], but are comparable with vertebrae from 'middle-sized' ichthyopterygian skeletons of ~3 m body length[1]. Their internal organization is also entirely cancellous incorporating a dense circumferentially oriented trabecular network (Figures 1C) that is compatible with 'adult' ichthyosaurian bone microstructure[6] (Figure S2) implying pelagic habits, accelerated growth, and elevated metabolism[1]. Such features are ubiquitous in advanced aquatic tetrapods and suggest that the earliest ichthyopterygian ancestors must have rapidly adapted as oceanic apex predators[1,2]. The new insight from PMO 245.975 is a closer stratigraphic proximity of specialized pelagic

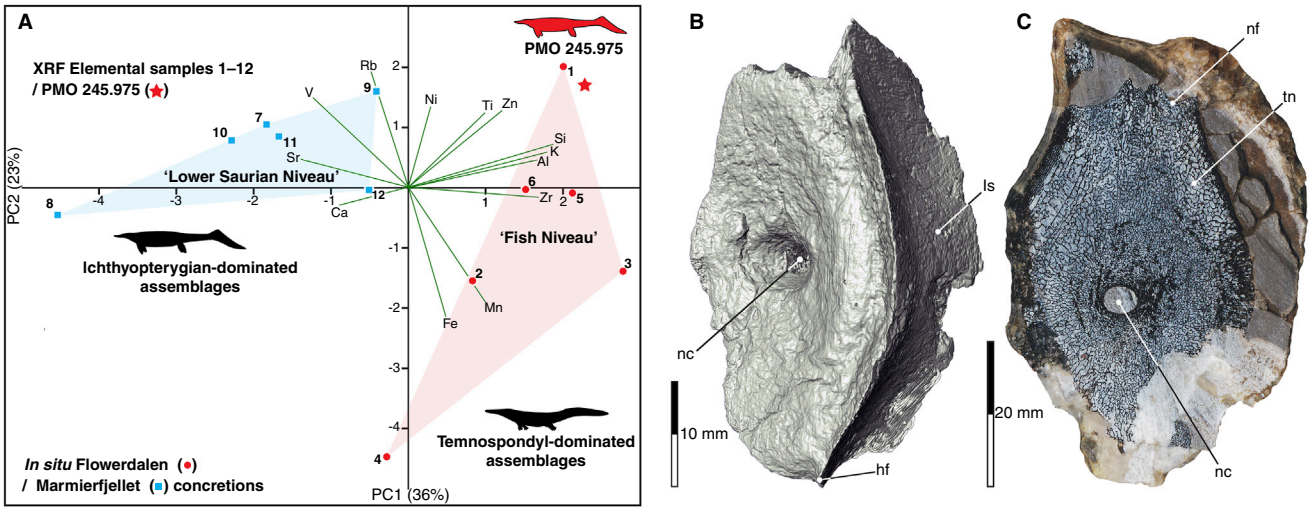

Figure 1. Stratigraphic context and morphology of the earliest ichthyopterygian fossils.
(A) XRF elemental geochemistry of calcitic matrix surrounding PMO 245.975 (red star) and *in situ* concretions from the 'Fish Niveau' along Flowerdalen (red circles) and 'Lower Saurian Niveau' on Marmierfjellet (blue squares). Elemental compositions and information for PMO 245.975 and samples 1–12 are listed on the open-access NIRD Research Data Archive (https://archive.sigma2.no/) under DOI:10.11582/2022.00058. (B) µCT image of a distal caudal centrum from PMO 245.975 in oblique view exposing the lateral surface. (C) Transverse section showing the densely cancellous internal bone structure. Abbreviations: hf, hemal arch facet; ls, lateral centrum surface; nc, notochordal canal; nf, neural arch facet; tn, trabecular network.

ichthyopterygians to the EPME. This recalibrates the traditionally assumed Mesozoic origin, land-to-water transition, and emergent radiation of not only ichthyosauromorphs, but also ichthyosauriforms and ichthyopterygians to both before the LSC[4] and within ~2 Ma of the Permian/Triassic boundary. Mean estimates for the initial ichthyosauromorph-ichthyosauriform divergence timescale range from ~1.7–17.7 Ma based on preferred phylogenetic and stratigraphic priors[2]. Consequently, we propose that these preludial marine reptiles most likely evolved before the EPME, but underwent opportunistic trophic niche diversification and ecological differentiation into shallower water amphibian-dominated versus deeper water ichthyopterygian-dominated habitats during the nascent dispersal of oceanic tetrapods in the earliest Triassic.

SUPPLEMENTAL INFORMATION

Supplemental information includes methods and two figures, which can be found with this article online at https://doi.org/10.1016/j.cub.2022.12.053.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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AUTHOR CONTRIBUTIONS

B.P.K. and J.H.H. conceived and designed the study, analysed the data, interpreted the results, and wrote the manuscript. J.H.H., V.S.E., Ø.H., and A.J.R. collected the specimens. V.S.E. and Ø.H. conducted the XRF analysis and interpreted the results. Ø.H. and A.J.R. undertook the µCT scans, segmentation, and rendering. All authors were involved in discussing the results and revising the manuscript.

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